Commentary on **Michael Domjan, Brian Cusato, & Ronald Villarreal (2000). Pavlovian feed-forward mechanisms in the control of social behavior. BBS 23(2):235–282.**

Abstract of the original article: The conceptual and investigative tools for the analysis of social behavior can be expanded by integrating biological theory, control systems theory, and Pavlovian conditioning. Biological theory has focused on the costs and benefits of social behavior from ecological and evolutionary perspectives. In contrast, control systems theory is concerned with how machines achieve a particular goal or purpose. The accurate operation of a system often requires feed-forward mechanisms that adjust system performance in anticipation of future inputs. Pavlovian conditioning is ideally suited to subserve this function in behavioral systems. Pavlovian mechanisms have been demonstrated in various aspects of sexual behavior, maternal lactation, and infant suckling. Pavlovian conditioning of agonistic behavior has been also reported, and Pavlovian processes may likewise be involved in social play and social grooming. Several further lines of evidence indicate that Pavlovian conditioning can increase the efficiency and effectiveness of social interactions, thereby improving their cost/benefit ratio. We extend Pavlovian concepts beyond the traditional domain of discrete secretory and other physiological reflexes to complex real-world behavioral interactions and apply abstract laboratory analyses of the mechanisms of associative learning to the daily challenges animals face as they interact with one another in their natural environments.

Learning theory, feed-forward mechanisms, and the adaptiveness of conditioned responding

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Abstract: The specific mechanisms whereby Pavlovian conditioning leads to adaptive behavior need to be elaborated. There is no evidence that it is via reduction in the "destabilizing effect that time lags have on feedback control" (Domjan et al. 2000, sect. 3.3). The adaptive value of Pavlovian conditioning goes well beyond the regulation of social behavior.

From the perspective of researchers who study learning processes, the target article is a highly original method of communicating to researchers in many fields how Pavlovian conditioning (PC) and operant conditioning interact to produce adaptive behavior. The Pavlovian mechanism provides a source of adaptive variants (selected by evolution) that are then honed by operant feedback mechanisms. The target article provides a new and, perhaps, more general language for discussing issues that have been treated by various theories of operant-Pavlovian interactions (Davis & Hurwitz 1977; Locurto 1981; Rescorla & Solomon 1967; Williams 1981). These issues include the influence of feedback on the form of the Pavlovian conditioned responses (Konorski & Miller 1937; Prokasy 1965) and the modulation of operant (Rescorla & Solomon 1967) and unconditioned responses (UR's) (Brown et al. 1983; Kimmel 1966) by Pavlovian conditioned stimuli (CS's). The emphasis in this article is on how the Pavlovian component contributes to the adaptiveness of behavior (cf. Hollis 1997; Prokasy 1965; Zener 1937). What is new in this presentation is the specific suggestion that the adaptive function of Pavlovian conditioning is to reduce the "destabilizing effect that time lags have on feedback control" (Domjan et al. 2000, sect. 3.3).

The target article does indeed present some good examples of the adaptive value of PC in the domain of social behavior. For example, it documents the role of sexual conditioning in reproductive behavior. It is evident that the Pavlovian CS decreases time to copulation (Domjan et al. 1998; Hollis et al. 1989; Zamble et al. 1985) and that CS exposure can even lead to greater competitiveness (Guttierez & Domjan 1996) and reproductive success (Hollis et al. 1997). However, it is not demonstrated that the adaptiveness arises via attenuation of a destabilizing effect of time lags. If there were a destabilizing effect of time lags, then we would expect to find some evidence of destabilization, such as increased behavioral variability, in those animals not exposed to the CS. In all of the examples cited, the average performance is enhanced by presentation of a Pavlovian CS, but there is no evidence of variability differences attributable to the Pavlovian experience.

The adaptive value of PC is broader than described in the target article (cf. Hollis 1997). For example, a very important function of PC is the production of specific outputs that are essential for inducing new behaviors during ontogeny. During behavioral development it is sometimes essential that a behavior occur in roughly accurate form the first time it occurs. Said another way, for feedback to be able to mold behavior into efficient forms it must first occur in a form that is a close enough approximation to the skilled response so that feedback can be effective. PC provides a feed-forward mechanism for this induction. For example, pairings of odor with tactile stimulation seem to underlie initial nipple attachment in rats (Pederson & Blass 1982; Petrov et al. 1999). Successful ingestion of milk seems to further contribute to the effectiveness of attachment (Petrov et al. 1999). The initial Pavlovian contingency gives rise to the behavior on which feedback operates. Another example of this comes from our own work on the development of independent feeding in ring doves. A Pavlovian contingency between the sight of seed and parental feeding induces thrusting at seed (Balsam et al. 1992; Deich & Balsam 1993). Beak opening is induced by the thrusting, and feedback from successful pecks molds the behavior into an adult coordination (Balsam et al. 1993; Deich et al. 1995). These behaviors are induced by PC that takes place during social interactions, and they influence future social feeding (Iskrant & Balsam 1994). In each case, the PC gives rise to a response that is then further modified by feedback.

The target article's unification of biological and learning theories stems from its specification of PC as one of the "proximate mechanisms that increase the utility of social behavior" (sect. 5). The results reviewed in section 4 and the additional examples that we cite above are supportive of this role for PC. But we take issue with the authors' contention that other such proximate mechanisms have yet to be specified by science. First, the adaptiveness of mechanisms that elicit social UR's, modal action patterns, and other species-typical social behaviors has been elaborated in many specific instances (Brown 1975). Second, Pavlovian conditioning is not the lone feed-forward mechanism in behavioral regulation. Habituation, sensitization, and imitation are all feed-forward mechanisms that can give rise to adaptive behavior forms prior to (and subsequent to) the operation of feedback (Balsam & Silver 1994; Balsam et al. 1998; Deich & Balsam 1994).

In conclusion, we agree that PC is an important mechanism of adaptive behavior but we would say that there is not enough evidence to conclude that its adaptiveness arises from a single control process – not even in the domain of social behavior.

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